THE DEVELOPMENT OF CONCEPTIONS OF PHOTOSYNTHESIS SINCE INGEN-HOUSZ

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THE various functions of a plant are so closely interdependent that it is impossible to study rationally any one activity without taking into consideration a number of others. It is constantly becoming more evident that imbibition, metabolism, growth, photosynthesis and transpiration are to a greater or less extent all interrelated, a study of the one requiring a knowledge of all the others. The physiological arrangements in vegetable organs are not obvious to the eye, they can be ascertained only by the application of a variety of methods, observational and experimental. These methods make use of a great number of different physical and chemical principles, the nature of which have been more or less definitely established, and in terms of which we now endeavor to interpret the actions of living things. The correlation of physical and chemical actions is of itself a difficult task, but when such actions have their seat of activity in living things, the task becomes tremendously difficult. Physiology is a great deal more than applied physics and chemistry. We must, however, rely upon these disciplines in order to form conceptions of the various vital phenomena, as operations of known causes. Thus these sciences have given us a vocabulary, while the true foundation of physiology will always be the direct observation of vital phenomena. The fundamental principles of the process of the utilization of the carbon dioxid of the air by the chlorophyllous leaf through the action of light, were established with almost no aid from physics and chemistry. Such an understanding of the phenomenon as we now possess has been possible only through the application of various physical and chemical facts. But photosynthesis is an exceedingly complex process, involving many factors and agents, all of which must be placed in proper relationship before a complete understanding can be hoped for.

It is not my purpose here to enter upon an elaborate historical discussion of the development of the ideas and theories relative to this subject. This is in itself a most fascinating and almost endless study, revealing often the most grotesque and

fanciful speculations of which the human mind has been capable. As in the history of every science, the carefully executed and exactly recorded experiments stand out as bright beacons to guide the workers in later generations. In no other way, perhaps, is the importance of reasoning only from careful experimentation and observation in order to gain light on the phenomena of nature brought home to one so clearly as by perusing the immensely prolix and speculative writings of most of the earlier workers. However, this fault is not entirely confined to our ancestors. In connecting the name of Ingen-Housz with the beginning of the development of photosynthesis, I do not mean to give all honor to one man. He stands as the representative of a group of highly-gifted investigators of a certain period and as is the case in all questions of this nature, each contributed a valuable portion to the whole. I purposely avoid discussion of the unfortunate and prolonged polemics which occurred at this time, a time-consuming study not altogether conducive to hero worship. However, from a plant physiological viewpoint and in the light of our present knowledge, the name of Ingen-Housz does stand out above his contemporaries as grasping the essentials of the cosmical function of plants. His little book of about 150 pages, "Experiments upon Vegetables," published 140 years ago, is one of the great classics of experimental plant physiology.

What then, briefly, was the status of the subject as found by Ingen-Housz and his contemporaries? Practically all of the work prior to this time was guided by the Aristotelian dictum that plants derive their nutrition from the soil. Against this mass of incongruous speculation there stand a few beautiful and classical observations. The great iatrochemist, van Helmont, endowed with extraordinary clearness of perception, denied the Aristotelian doctrine of the composition of organic matter and considered water the chief constituent thereof. His classical experiment is probably well known to all. In a pot he placed 200 pounds of thoroughly desiccated soil and planted therein a willow twig weighing 5 pounds. This was protected from dust and watered daily with rain-water. After five years the plant had enlarged greatly, and increased in weight by 164 pounds, while the earth, after desiccation, showed a loss of only 2 ounces. And almost three hundred years later Liebig was still fighting the humus theory of nutrition!

Probably the first to express the idea that the leaves are the organs which produce the substances necessary for the develop-

ment of the plant was the Italian, Malphigi, in the seventeenth century. He considered the chief function of the leaves to be the digestion of the nutrient sap rising from the roots. This process of digestion in the leaves was considered essential for the development of the plant, as was shown by the deleterious effect of removing the cotyledons (which he regarded as true leaves). He noticed, furthermore, that in the leaves are openings, "which," he says, "pour out either air or moisture," though it is quite evident that Malphigi did not recognize the other function of the stomata, namely, the absorption of gases. Grew in 1676 also pointed out the existence of stomata.

In considering the work on photosynthesis of this time, it must be borne in mind that the most confused and contradictory opinions prevailed as to the composition of the atmosphere. It is difficult to imagine the chaos which existed on a subject which now seems to us so simple. All the more remarkable are the observations of that brilliant investigator, Stephen Hales. He concluded that plants draw some part of their nourishment through their leaves from the atmosphere, and he was also the first to suggest the influence of light. A contemporary of Newton, Hales regarded light as a substance and asks "may not light which makes its way into the outer surfaces of leaves and flowers contribute much to the refining of substances in the plant?"

And finally there may be mentioned also the observations of Bonnet, who was the first to record the evolution of gas from submerged illuminated leaves, but he was not able to interpret properly his observations.

Priestley had noticed that plants confined in an atmosphere rich in fixed air (carbon dioxid) produced in the course of some time large quantities of dephlogisticated air (oxygen). Priestley explained the phenomena as caused by the growth of the plant and elaborated his discovery in relation to the cosmical function of vegetation. Schelle, working in Sweden, who had discovered oxygen simultaneously with Priestley, reported quite the opposite results; his plants produced fixed air (carbon dioxid) and he challenged the correctness of Priestley's results. On repeating his investigations, Priestley himself became confused through the irregular outcome of his experiments, looking always simply to the growth of the plant, and finally practically refuted his original statement.

Jean Ingen-Housz, an eminent physician, interested primarily in the influence of foul and pure air on the health of man, became enthused by the reports of the influence of oxygen

on living things. Schelle had shown that atmospheric air was composed of about[1] two parts of nitrogen, one part of oxygen and a small quantity of carbon dioxid. But the latter gas was also considered an element, though it was known that it was exhaled by animals, as was also its physiological property that it would not support life. Ingen-Housz was started on his investigations by Priestley's announcement that growing plants produce oxygen. He was, however, much more fortunate than Priestley in his experimentation. He soon saw that the mere growth of a plant had nothing to do with the purification of the air. His experiments are a masterpiece of manipulation and self-criticism. Step by step he approached the correct interpretation. It was the effect of the sunlight on the plant which produced the oxygen and this was due to the light, not the heat, which the sun radiates; and only in the light did the action take place, while the green leaves only were capable of this action. The carbon dioxid came from the atmosphere and the oxygen escaped through the stomata. High concentrations of CO_2 were toxic to the plant, and in the dark or even in the shade, not oxygen, but CO_2 was evolved. The contradictory results of Priestley and of Schelle were explained. Thus did Ingen-Housz grasp the very fundamentals of the process.

In 1784 Lavoisier established the composition of carbon dioxid and the nature of combustion. At this time the battle of opinions regarding these processes was at its height, and the value of Lavoisier's discovery was unheeded even by Ingen-Housz. But in his second publication he saw the matter clearly. The source of the oxygen was the carbon dioxid, the combustible matter of the plant was thus formed, van Helmont's experiment was explained, and the organism was seen to live by the burning of the material which it had itself formed. But there were also contributions from other workers; none of them, however, had the same clarity of vision and could distinguish between the two functions proceeding simultaneously, photosynthesis and respiration, nor made use of the modern conception of the composition of carbon dioxid. Sénébier executed extensive experiments and published voluminous elaborations. He showed how photosynthesis was affected by temperature, and by means of his well-known colored bell jars ascribed the chief action to the red rays of the spectrum. But the old Aristotelian dictum persisted; the roots were supposed to supply the leaves with solu-

[1] Black, Joseph, "Lectures on the Elements of Chemistry," 1st Am. ed. from last London ed., 1806, 2: 344.

tions of carbon dioxid. This was not definitely eradicated until the work of Moll and of Bousingault with pure water cultures.

As in all questions of this nature, so here it is also almost impossible to definitely establish who was the first to observe the utilization of carbon dioxid by the plant. Technically the honor probably belongs to Henry and Persival, though our present knowledge undoubtedly comes directly from Ingen-Housz and Sénébier. Although Ingen-Housz clearly described the phenomenon of CO_2 evolution both aerobically and anaerobically, it is surprising how long the erroneous conceptions regarding these processes persisted.

And finally to this period belongs the work of de Saussure. Though a contemporary of Ingen-Housz, Sénébier and Priestley, de Saussure attacked the problem a few years later. Perhaps nowhere else is there such a clear example of the tremendous change which had been wrought by the new chemistry of Lavoisier. From the style of thought and presentation, there might be a century between de Saussure and his contemporaries who had worked on this problem. De Saussure's conceptions of the composition of air, the nature of burning and the composition of water were clear and based upon definite experimentation. He worked entirely quantitatively; he asked a certain question and got a definite answer, and thus he established the quantitative relations of the phenomena which Ingen-Housz, Priestley, Sénébier and a few others had described, besides several new discoveries, more especially the rôle which water plays in the process of photosynthesis. De Saussure spoke a new language and followed a new system of thought. In fact, his work naturally would mark the beginning of a new era. But alas, it also marks the beginning of a rapid decline, both in investigation and in the presentation of existing knowledge on the whole subject of plant nutrition. A perusal of the textbooks as they appeared from about 1815, with a very few exceptions, reveal such unpardonable inaccuracy, indifference and simple ignorance as to be quite incomprehensible in view of the enormous importance of this phenomenon to human welfare. Most of the modern texts of plant physiology and physiological chemistry by no means escape this criticism. The beautiful experiments of the men just referred to were either forgotten or directly misinterpreted. The works of Dutrochet, Sachs and Pfeffer may be cited as the few great exceptions.

Aside from the discovery of certain details of the process of photosynthesis regarding the easily detectable products and the influence of certain exterior factors, the status of our knowledge is practically as de Saussure left it over 100 years ago!

What then are the causes of this lamentable stagnation, this apparent indifference to a branch of science which deals with a phenomenon upon which our very existence depends? It is not, I believe, to any one cause or condition that the situation can be attributed. We are not guilty of following an erroneous doctrine or system of thought. But the difficulty rather lies in the great complexity of the subject itself.

Among the botanists of the time the discoveries of Ingen-Housz and his contemporaries found no interest. This was at the time when Linné determined the course of botanical thought. There was at the time no such discipline as plant physiology; Hales, Ingen-Housz, Priestley, Sénébier, de Saussure were not botanists, but physicists and chemists. Here is an example of the deplorable results arising from the unfortunate sharp division of the various fields of science. Botany was not developing a symmetrical structure, but a highly lopsided one with attention restricted to the description and classification of plants. Cuvier, the great academician, one of the most illustrious men of that glorious age when France was truly the home of science, who did so much for botany, especially for its wide study and culture, utterly neglected the functional and nutritional phase. Nor did Humboldt, in spite of his unusual versatility and enormous influence in the world of science, affect the course of this subject beyond writing an introduction to the German translation of Ingen-Housz's work. The writings of Schleiden and of Liebig certainly did much to improve the conceptions of nutritional science of the day, but their efforts were entirely critical and not experimental, hence no real contributions resulted from their efforts; while such men as Mohl, Nageli, Hofmeister and Darwin were also following other lines of thought. The experiments of Bousingault do stand out clearly at this period. He finally demonstrated with his method of water culture the true source of carbon for the plant, as well as the fact that atmospheric nitrogen is not directly taken up by the plant.

Sachs through his studies of chlorophyll function awoke new interest in the subject. His work on the formation of starch, as well as that of Böhm on the effect of sugars on starch formation, has led to an extended elaboration of this phase of the subject. And finally Wm. Draper of New York conducted extensive investigations on the effect of different portions of the spectrum on the evolution of oxygen, the results of whose work have been verified and extended by the studies of Pfeffer. Most of the botanical contributions of the last thirty years have been largely confined to detailed studies along the courses outlined by these workers. It is not detracting from their value to say that

no new vistas have been opened nor original hypotheses formulated.

During the period just reviewed, all branches of science experienced development and revolution beyond all precedent in the history of thought. A discovery in one domain of science often exerted great influence over its allied or even distantly related sciences. We need but recall how the Newtonian gravitation formula affected not only astronomy and physics, but chemistry and physiology. During this time such fundamental conceptions as the conservation of energy, the undulatory theory of light, spectrum analysis, entropy and the primary laws of photochemical action were formulated, all of the most direct importance to the problem of photosynthesis. These great discoveries have even now found little application to our subject.

The most important aspect of the problem of photosynthesis is probably the energy relation. By virtue of this photochemical action we are kept alive, we derive all of our food, we keep warm, travel, and run our industries, by the use of fossil energy, coal. It is this question of energetics which in spite of some of the excellent attempts which have been made, has hardly been touched, and lies at the very center of the problem at least from a humanitarian viewpoint. As Boltzman pointed out in his classical paper on the second law of thermodynamics, the struggle for existence is essentially not a fight for the raw materials, which are abundant in earth, sky and sea, nor for the energies as such, but for the potential energies as in coal, sugar and meat.

It would seem that the plant itself is not very efficient in the utilization of this energy, and certainly our methods of determining the values have been anything but satisfactory. This is largely due to the number of variable factors entering into the experiment and calculation. The determinations of Puriewitsch may serve as a good example. The light was measured by means of a bolometer, and the amount of photosynthate or material synthesized was determined by the half-leaf method. The energy of this material was determined from the heat of combustion.

	Before Isolation	After Isolation
Area of half leaf	316.6 sq. cm.	316.8
Dry weight of half leaf	1.2494 g.	1.3952
Dry weight per sq. cm.	0.0039	0.0044
Heat of combustion of 1 g. dry weight	4300.21 g. cal.	4313.46 g. cal.
Heat of combustion per sq. cm.	16.770	18.978
Increase of heat of combustion after insolation per sq. cm.	2.208 g. cal.	
Total energy fall on leaf	361.03 g. cal.	
Energy used in assimilation	0.6 per cent.	

The values for the energy utilized vary greatly, from 0.6 per cent. to 5.0 per cent. with the same and different kinds of plants. One of the great difficulties has been that we do not yet know with what sort of system we are dealing. It is quite clear that it is not one simple chemical reaction, but a series into which various factors enter, and in some of which light plays the leading rôle. So that as the results indicate, these values are the merest approximations. In fact, the old question how does light act in effecting the reduction of carbon dioxid and water, seems almost as far from solution as ever. It is still an open question whether we are dealing with a so-called photo-catalytic action in which light only accelerates an irreversible process, in which case we cannot regard the energy of light as being stored in the transformed substance, or whether it is a true photochemical action. One great difficulty here has been that the physicists themselves have not been unanimous in accepting the theoretical principles of radiant energy and its relation to chemical action.

Recent conceptions of the nature of light and of chemical forces ought to find application to the processes involved in photosynthesis. It seems highly probable that the forces of chemical affinity are electrical in character, and matter may be regarded as a complex structure of small particles, the atoms, together with very much smaller particles called electrons. The number of electrons which accompany an atom to a large measure determine its chemical properties; valency under this conception depends upon the relative ability of the atoms to eject or attract electrons, and the chemical effects produced by light are due to the emission of electrons from some of the atoms of the illuminated substance. Each electron always has a negative charge of electricity and is therefore attracted towards all positive charges. Under certain conditions some substances lose electrons and acquire a positive charge. Thus there are a number of metals which when exposed to the rays of ultra-violet light take on a positive charge, and this has been traced to the emission of the negative electrons from the illuminated surface. The phenomenon is known as the photoelectric effect, and has been observed in a large number of substances, including a variety of dyes. There is considerable evidence for believing that the valency electrons which are the chemical bonds in molecules, are identical with the photoelectric electrons which can be liberated by the action of light. From this point of view, a photochemical change and a photoelectric change are of the same character, consisting primarily in the loss or displacement of an electron through the absorption of energy from a light

wave. It is not possible here to enter upon a discussion of the photochemical laws, but it seems quite certain that the first stage in any photochemical reaction consists essentially in either the partial or complete separation of negative electrons which are either emitted or attach themselves to other chemical groups or atoms. There takes place thus a rearrangement of the energy distribution in the system which, of course, involves chemical changes.

The phenomena of oxidation and reduction may be interpreted upon the same basis. Thus, for example, the oxidation of ferrous sulphate with bromine water may be represented:

$$2\overset{++}{Fe} + 2\overset{--}{SO_4} + \overset{+}{Br_2} \rightarrow 2\overset{+++}{Fe} + 2\overset{--}{SO_4} + 2Br.$$

The ferrous salt is "oxidized" to a ferric salt and the bromine "reduced" to a bromine ion. It will be noticed that the "oxidation" (I purposely retain the old terminology) involves the passage of a positive charge to the ferrous ion, the bromine being the oxidizing agent, or the ferrous salt the reducing agent. There cannot be oxidation without corresponding reduction, and reduction consists essentially in the loss of a negative charge. Oxygen acts as an oxidizing agent because it has a great tendency to take away a negative charge from other substances and go over into electronegative oxygen of a compound, usually water. In photosynthesis the process is quite the reverse. If we assume that the action is empirically:

$$XCO_2 + XH_2O \rightarrow (CH_2O)_x + XO_2,$$

water is oxidized and CO_2 is reduced presumably to carbohydrates and the negative charges are taken up by the carbon compounds. Thus photosynthesis must be accompanied by decided electrical disturbances and of a nature which are in a sense the reverse of those taking place in the oxidation of food material. This furnishes us with a point of attack and possible basis for the explanation of the electrical disturbances characteristic of living things. As yet no application has been made of these principles, though it is noteworthy that the atmosphere surrounding a leaf is ionized and Waller has described certain electrical disturbances in the leaf. These are apparently associated with the photosynthetic activity, for the action ceases on the removal of CO_2, and is not brought about by light which has been filtered through a green leaf.

McClelland and Fitzgerald have recently observed that

green leaves in the light of an aluminium arc exhibit a decided photoelectric discharge, as do also aqueous solutions of chlorophyll. I have tried to detect such an effect by the use of sunlight, but have never succeeded. It would seem that the electrons are emitted only under special conditions, and ordinarily are probably attached to the escaping oxygen or water vapor.

The application of physical conceptions and methods of experimentation as yet have not been applied to the study of photosynthesis with any high degree of success in penetrating to a clearer view of the process. This to a large measure has been due to the fact that our knowledge of the chemistry of the process has been so very fragmentary. The physical investigations have indicated that the process is apparently not a simple one, but dependent upon a number of variable factors. Physics employs essentially quantitative or mathematical forms of expression. But before quantitative terms can find expression, it is essential that at least a certain amount of qualitative knowledge is existent. We must know, at least, whether a proposition is affirmative or negative; some elements of the hypothesis must be established. Thus it was possible for de Saussure to apply quantitative methods to the discoveries of Ingen-Housz and Sénébier, but our qualitative knowledge has not progressed much beyond the discoveries of these men. Sachs elaborated the observations of Mohl on the starch grains and thereby introduced the subject of sugar chemistry into the process. It became then distinctly a chemical problem.

The course which the development of chemistry took was influenced by a number of factors. It is evident that science has progressed essentially by the efforts of a relatively few individual thinkers who set the minds of many working in certain directions, and that science, like social and political institutions, is not above the influence of fashions which have been followed by the majority, and often not altogether to the advantage of the broad development of knowledge. At the time of Liebig organic chemistry was devoted to the study of the chemistry of living things. But with the discovery of the constantly increasing number of carbon compounds and under the leadership of men like Victor Meyer, Kekulé, Hofmann and Baeyer, the primary interest was shifted to theoretical considerations of constitution and structure. Combined with this, the effect of the lure of the commercial application of synthetic products and the development of new processes, forced the study of chemistry of the phenomena of nature into second place. Physiological chemistry with relatively few disciples was de-

voted largely to animal investigation. And it is only within rather recent times that there has been a return to what might be termed general physiological chemistry with the plant studies in the decided minority.

Probably as a result of this state of affairs on the educational system, the contributions of the chemists to the problem of photosynthesis have not been of the thorough and profound nature which the subject demands. Most of the suggestions of the chemists concerning the course of the process have been purely hypothetical and speculative, exhibiting the most lamentable ignorance of the fundamental character of the process, and often with total disregard of the structure of the chlorophyllous cell and the properties of living matter. It is not surprising, therefore, that many botanists paid little attention to these efforts and few cooperative efforts were undertaken.

From the chemical viewpoint, the salient fact regarding the process of photosynthesis is that carbohydrates are the first products which accumulate in sufficient quantity for detection. It is by no means established in what manner these substances are formed, but as the formation of sugars has been found to accompany the process almost universally and the course of accumulation has been extensively studied, they have come to be regarded as the first visible products. The sugars then stand in the very center of the food economy of plants.

Before discussing the subject of the sugars themselves let us consider very briefly the manner in which these are supposed to be formed in the chlorophyllous cell. This portion of the problem has not advanced beyond the purely hypothetical stage, although it is very frequently treated as though the principle had been firmly established. The theory which has received the greatest recognition, and, it would seem, almost universal acceptance, is the formaldehyde theory. This hypothesis was formulated by Baeyer as a mere suggestion. During the fifty years since its appearance, this suggestion has become almost an axiom. It might be desirable, therefore, to examine briefly the evidence upon which this theory rests in order to determine whether its widespread acceptance is warranted by experimental proof.

In 1861 Butlerow had discovered that formaldehyde, in aqueous alkaline solution, condenses to an optically inactive syrup, possessing some of the properties of hexose sugars. Baeyer considered formaldehyde in aqueous solution to be $CH_2(OH)_2$, and the Butlerow condensation as simply one of water loss and condensation of six $CH_2(OH)_2$ molecules.

$$6CH_2(OH)_2 - 6H_2O \rightarrow COH \cdot (C(OH)H)4 \cdot CH_2OH.$$

Baeyer then suggested that this may be the way in which grape sugar is formed in the plant. The idea of the similarity of chlorophyll and hemoglobin was prevalent at the time; it seemed, therefore, likely that chlorophyll should also fix CO. The sunlight splits the CO_2 into CO and O, the oxygen escapes, and the carbon monoxide, held by the chlorophyll, is reduced to formaldehyde, $CO + H_2 \rightarrow COH_2$, which is then condensed to sugar. This is the substance of the Baeyer hypothesis, formulated without the support of experimental evidence. It was proposed as a possibility and received no further attention in the writings of its founder.

The fact which more than any other gave strength to this theory, and which is the underlying principle of the whole idea, was the discovery of Butlerow. This discovery was elaborated by O. Loew, who gave the name formose to the sugar mixture, and especially by Emil Fischer, who prepared therefrom some of the sugars found in nature.

The hypothesis has to a great extent directed the course of investigation of the chemical aspect of photosynthesis. The experiments have followed three different lines of argument:

(1) The reduction of carbon dioxid to formaldehyde by various chemical and photochemical means. (2) The detection of formaldehyde in illuminated green leaves. (3) The feeding of plants with formaldehyde as the only source of carbon.

All of these have yielded direct positive results, although it is impossible to give a description of the very numerous experiments. The main points at issue are, however, whether we are justified in applying the results of experiments carried out *in vitro* or under other abnormal conditions, to the living plant, and whether the conditions in the experiments simulate sufficiently those existent in the chlorophyllous cell to permit of valid deductions. In spite of the very numerous contributions which have been made to this special subject, a critical study of all the facts leads to the conclusion that it will require a great deal more experimental substantiation before this theory can serve as the basis for an explanation of the mode of sugar manufacture in the leaf.

Although Sachs had identified the formation of starch in the chloroplasts with the photosynthetic activity, it was later recognized by Meyer that many leaves never form starch. In the latter case there is an accumulation of cane sugar. Boehm then found that in either kind of leaf there was an accumulation of starch or sugar when the leaves were placed on solutions of glucose or fructose. The question has then naturally arisen as to

what is the first sugar formed in photosynthesis. This is, of course, an immensely important problem, as its solution would throw much light on the chemics of the photosynthetic process. As yet no definite solution has been gained, and the results are by no means concordant. The conclusions have been drawn largely from a consideration of the variation in amount of different sugars and from microchemical tests. The latter can not be considered sufficiently accurate to differentiate positively between various sugars. The following are the results of Brown and Morris with the garden Nasturtium, and serve as the best illustration. The values represent percentages of the dry weight.

Carbohydrate	Picked and Dried 5 A. M.	Picked 5 A. M. Kept Insolated in Water Until 5 P. M.	Picked and Dried 5 A. M.
Starch	1.23	3.91	4.59
Sucrose	4.65	8.85	3.86
Glucose	0.97	1.20	0.00
Fructose	2.99	6.44	0.39
Maltose	1.18	0.69	5.33
Total sugar	9.69	17.18	9.58

Carbohydrate	Picked and Dried at Once	Leaves Kept in Water in Dark for 24 Hours After Picking
Starch	3.69	2.98
Sucrose	9.98	3.49
Glucose	0.00	0.58
Fructose	1.41	3.46
Maltose	2.25	1.86
Total sugars	13.64	9.39

From these results Brown and Morris conclude that cane sugar is the first sugar formed in the leaf, and that it is a temporary reserve material which accumulates during active photosynthesis. When the cane sugar reaches a certain concentration, an excess is converted into starch. Prior to translocation, the cane sugar is inverted into glucose and fructose. The fact that leaves which are photosynthetically active all day contain no glucose or fructose is used by Brown and Morris as an argument that these can not be the first sugars formed. In the cut leaf insolated in water, translocation has presumably been stopped, and they point out that cane sugar and starch both increase greatly, but glucose very little. Fructose, the other hexose, it should be noted, however, increases decidedly.

One factor which has been overlooked in these considerations is the transformation of the various groups of sugars quite independent of the process of photosynthesis. This mutual

transformation is of the nature of a complex equilibrium with the monosaccharides as one extreme, and starch as the other, controlled, in all probability, by enzyme action. This equilibrium is affected by various influences, more particularly by the water content of the system and temperature. It is evident then that the amount, or proportion to the total of certain sugars present in the leaf after insolation, can not be taken as an indication of the rate at which these sugars are formed in the photosynthetic process, for under varying conditions of water content and temperature, such as occur in a leaf in the sunlight, there is a consequent shifting of the carbohydrate equilibrium, resulting in the accumulation of one or the removal of another group of sugars according to circumstances. Therefore, in a study of the first sugar formed in photosynthesis, these conditions (water content and temperature) either must be kept constant or, what is more feasible, the equilibrium under the particular circumstances must be established before any conclusions can be drawn as to the immediate source of any particular sugar.

The fleshy joints of some of the cacti have offered splendid material for studies of transformation of the sugars. These plants are capable of large variation in their water content, the joints can be removed from the plants and subjected to a variety of conditions without injury. Thus two sets of joints were kept at different temperatures in the dark for twenty days and then analyzed. The values are percentages of the dry material.

	28° C.	10–15° C.
Dry weight	33.0	33.6
Total sugars	5.72	6.21
Total polysaccharides	5.28	5.59
Hexoses and disaccarides	0.40	0.60
Total hexose sugars	2.17	2.38
Disaccharides	0.26	0.32
Hexoses	0.16	0.27
$\frac{\text{Total polysaccharides}}{\text{Total sugars}}$	.913	.900
$\frac{\text{Hexoses}}{\text{Hexose polysaccharides}}$	.0884	.147
$\frac{\text{Hexoses and disaccharides}}{\text{Total sugars}}$	.069	.0966

It is evident then that in general a low temperature tends to shift the equilibrium in the direction of the simpler sugars.

Similar relations hold for the effect of the water content. The table below gives the results of two sets of joints, one set (A) kept dry, the other (B) given water:

	A	B
Dry weight	22.80	17.70
Total sugars	18.84	18.58
Total polysaccharides	16.21	15.77
Hexoses and disaccharides	.56	.81
Total hesose sugars	8.43	7.81
Disaccharides	.30	.36
Hexoses	.26	.45
$\frac{\text{Total polysaccharides}}{\text{Total sugars}}$	.861	.849
$\frac{\text{Hexose}}{\text{Hexose polysaccharides}}$	.032	.063
$\frac{\text{Hexoses and disaccharides}}{\text{Total sugars}}$	.0297	.0436

Thus the water content of a leaf decidedly affects the nature of the sugars, and in such a manner that decreasing water content shifts the equilibrium in the direction of the more complex or more condensed sugars, while ample water brings about inversion or the formation of the simpler sugars. In the pentose series the action is of the same nature. It is a noteworthy fact that the water content does not seem to affect the rate of respiration as measured by CO_2 evolution.

Unfortunately in the results of Brown and Morris and the other workers who have investigated the problem of the first sugar, not sufficient data are given regarding leaf temperatures and water content. These factors when considered in the light of the results just given would materially affect the interpretation of the analyses.

The examples given here illustrate to some degree the complexity of the problem of photosynthesis. The enormous importance of this phenomenon to human welfare needs no elaboration. Progress undoubtedly lies in the fortunate cooperation and application of the methods and concepts of various branches of science; botany, physiology, chemistry and physics. The dangers lie in the over-application of physical and chemical theories based on restricted observation and acquaintance with the phenomenon itself.